A revision of *Gyrocochlea*-grade Charopidae from mid-eastern Queensland and redescription and generic reassignment of three *Gyrocochlea*-grade species (Eupulmonata: Charopidae)

Lorelle HOLCROFT

School of Environment and Science, Griffith University; Australian Rivers Institute. Email: lorelle.holcroft@ griffithuni.edu.au; lorelle.holcroft@bigpond.com

Citation: Holcroft. L. 2018: A revision of *Gyrocochlea*-grade Charopidae from mid-eastern Queensland and redescription and generic reassignment of three *Gyrocochlea*-grade species (Eupulmonata: Charopidae). *Memoirs of the Queensland Museum – Nature* 61: 1–28. Brisbane. ISSN 0079-8835 (Online), ISSN 2204-1478 (Print). Accepted: 14 January 2018. First published online: 30 April 2018

https://doi.org/10.17082/j.2204-1478.61.2018.2017-14

LSID urn:lsid:zoobank.org:pub:8D81529E-3CA8-44FA-9AAB-6C63201074C9

ABSTRACT

This study reviews the *Gyrocochlea*-grade charopid snails of mid-eastern Queensland. *Gyrocochlea auct.*, characterised by brown, biconcave shells with a diameter of 3-7 mm, has been shown to be polyphyletic (Shea *et al.* 2010). *Gyrocochlea s.s.* is confirmed as a genus geographically restricted to the Border Ranges of south-east Queensland and north-eastern New South Wales (Stanisic 1990). This study utilised scanning electron microscopy of the shell architecture, qualitative and quantitative measurements of conchological features and anatomical dissection where suitable specimens were obtainable. Based on shell morphology, primarily protoconch sculptural patterns (as defined in Holcroft 2018), this study re-assigns three *Gyrocochlea*-grade species, *G. chambersae* (Stanisic, 2010), *G. iuloidea* (Forbes, 1851) and *G. danieli* (Stanisic, 2010) to three new genera, *Stanisicaropa* gen. nov., *Whitcochlea* gen.nov. and *Radiolaropa* gen.nov. respectively and diagnoses four new genera, *Amfractaropa* gen.nov., *Comularopa* gen.nov, *Nodularopa* gen. nov., *Amfractaropa* bretti sp. nov., *Comularopa* georginae sp. nov., *Radiolaropa* eungella sp. nov., and *Xenoropa* wigtonensis sp. nov. \Box *Mollusca, Eupulmonata, Charopidae, Gyrocochlea, protoconch* sculpture, new genera, new species.

The Charopidae (Pinwheel Snails) is a speciose family of tiny snails (shell diameter from 1-7 mm) of Gondwanan origin (van Bruggen 1980) inhabiting rainforest environments of many of the land masses of the Southern Hemisphere but is particularly diverse in eastern Australia (Queensland, New South Wales, Victoria and Tasmania). The family does occur, but less frequently, in South Australia, Western Australia and central Australia (Smith 1992; Stanisic *et al.* 2010, 2017). Of an estimated 750 Australian charopid species, only approximately 25% have been described, causing a taxonomic backlog within this family which needs to be resolved (Hyman & Stanisic 2005; Stanisic *et al.* 2010, 2017; Shea *et al.* 2012; Stanisic 2016).

A major group of charopids in eastern Australia are the *Gyrocochlea*-grade species (Stanisic 1990; Stanisic *et al.* 2010; Shea *et al.* 2012; Holcroft 2017, 2018). *Gyrocochlea*-grade charopids are a group of species characterised by typically brown, biconcave shells with a diameter of 3–7 mm (generally less than 5 mm) and a strong, radially-ribbed teleoconch (Shea *et al.* 2012). Species inhabit rainforests, both wet and dry, where they play a significant role in maintaining the environmental health of the ecosystem (Stanisic 1990, 1998). Species prefer to live under logs, rocks and in the leaf litter of rainforests (Bishop 1981; Stanisic 1994; Stanisic & Ponder 2004; Hyman & Stanisic 2005).

From an initial 11 species of *Gyrocochlea* described by Hedley (1924) the number had grown to 34 species in Stanisic *et al.* (2010) which included 22 newly described. Shea *et al.* (2012) in a molecular and morphological study of *Gyrocochlea* showed that *Gyrocochlea* sensu stricto was in fact restricted to a small number of species from Border Ranges of NE NSW/SEQ. Consequently eight new genera were diagnosed to accommodate 17 new and 9 previously described *Gyrocochlea*-grade species from mid-east and north-eastern NSW. Subsequently Stanisic (2016) reassigned '*Gyrocochlea*' myora Stanisic, 2010 from North Stradbroke Island, SEQ to a new genus.

Historically, *Gyrocochlea*-grade charopids have been known from mid-eastern Queensland (MEQ) since the 1840s with 'Gyrocochlea' *iuloidea* described from Long I, (= Port Molle) in the Whitsunday islands by Forbes in 1851. Hedley (1912) added 'Gyrocochlea' recava which Stanisic (1990) subsequently reassigned to a new genus Biomphalopa. Stanisic et al. (2010) described 9 species of pinwheel snails from the region including three new species of *Gyrocochlea*-grade charopids. However, recent investigations of the land snail collections of the Queensland Museum (Brisbane) by the author revealed an additional number of putative species of Gyrocochlea-grade charopids from MEQ that have yet to be described.

This study revises three '*Gyrocochlea*' species from MEQ introduced by Stanisic *et al.* (2010). All three species are assigned to new generic units based on their protoconch sculpture which differs significantly from true *Gyrocochlea* (type species. *Helix vinitincta* Cox, 1868). In addition, five new genera and species

of *Gyrocochlea*-grade charopids from MEQ are described with protoconch sculpture also differing substantially from true *Gyrocochlea*. *Biomphalopa recava* (Hedley, 1912) has been included in this study as a MEQ *Gyrocochlea*grade species originally separated from *Gyrocochlea* s.s. by Stanisic (1990).

Delimitation of charopid genera and species

From a morphological perspective, determining generic difference in Australian Charopidae has been primarily based upon protoconch architecture (Stanisic 1990; Bonham 2003; Hyman & Stanisic 2005; Shea et. al 2012; Stanisic 2016; Holcroft 2018) in combination with shell coiling pattern and teleoconch sculpture. While spiral, radial and reticulate protoconch sculptures were used previously (Iredale 1937ab; Smith & Kershaw 1979; Stanisic et al. 2010; Shea et al. 2012), the more rigorous classification system and nomenclature for protoconch sculptural patterns prescribed by Holcroft (2018) provide a consistent and informative terminology in the descriptions presented in this study. Eleven major configurations of protoconch microsculpture were identified by Holcroft (2018) of which four have been applied to taxa included on this study.

Secondarily, the size and structure of genitalia may be also used to delimit genera. However, this is largely dependent on the availability of suitable material for dissection.

In the absence of animal tissue suitable for reliable molecular analysis and comparative anatomical analyses, species delimitation in this study has been based on shell morphology with the exception of two species where anatomical dissection was possible. Charopidae with very minor exceptions are rich in shell characters useful in species delimitation. Solem (1983) established criteria for such an approach. He recognised that to maintain genetic integrity, species must possess certain 'species recognition' features in the reproductive organs. In particular, Solem indicated that penial structure (size of penis and the number, shape and length of internal pilasters) was significant in this regard. Solem also found that major differences in reproductive anatomy correlated with measurable conchological differences. This was based on the premise that genetic divergence is reflected in phenotypic alterations of the shell. As a result, Solem (1983) proposed that at least 3 non-correlated conchological differences must exist for allopatric populations to be classified as distinct species.

In this paper, strong emphasis has been placed on a number of conchological features such as shell coiling pattern, shell diameter, number of ribs on the body whorl, ratio of shell diameter to umbilical width (D/U), ratio of shell height to diameter (H/D) and number of whorls to distinguish species. In addition features relating to gross shell morphology and teleoconch sculpture (radial rib structure, rib spacing, microsculpture) have also been examined in detail.

ABBREVIATIONS

General. SEM, scanning electron microscopy; SC, spirit collection; RC, dry collection.

Institutions. AM, Australian Museum, Sydney; NHM, Natural History Museum, London; QM, Queensland Museum, Brisbane.

Habitat Data. alt., altitude; Ck, Creek; CNVF, complex notophyll vine forest; Hts, Heights; I., Island; Mts, Mountains; NVF, notophyll vine forest; R., River; Ra., Range; SEVT, semi-evergreen vine thicket; SNEVF, simple notophyll vine forest; MEQ, Mid-eastern Queensland; NENSW, Northeastern New South Wales; NEQ, North-eastern Queensland; WT, Wet Tropics; NP, National Park; NSW, New South Wales;. SEQ, Southeastern Queensland; SF, State Forest.

Shell features. AH, aperture height; AW, aperture width; D, shell diameter; H, shell height; PD, protoconch diameter; T1, 1st whorl of the teleoconch; UW, umbilical width; WWB, number of ribs on the 3rd quarter of the body whorl.

Anatomical data. E, epiphallus; EP, epiphallic pore; P, Penis; PP, penial pilasters; PRM, penial retractor muscle; PS, penial sheath; VD, vas deferens.

MATERIALS AND METHODS

The study was chiefly based on material held in the Queensland (Brisbane) and Australian (Sydney) Museums. Individual specimens are identified by their registration number and respective institutional prefix (QMMO, Queensland Museum; AMSC, Australian Museum) and the private collection of Jack Worsfold (JW). Supplementary field work was conducted to collect further animal tissue suitable for dissection.

Morphological methods. Adult shells were measured using a Camera Lucida mounted on a WILD M5 stereo microscope. Measurements were converted from ocular micrometer units to mm using a conversion factor at a set magnification. Characters investigated included shell shape, size (height and diameter), whorl count, coiling pattern, rib count and umbilical width (Appendix 2). Standard definitions (Solem 1983) for most conchological characters were used and whorl counts were made to the nearest 1/8 whorl.

High resolution images of shells (260-600MB) were obtained using a Visionary Digital BK-Plus lab system camera set-up in the Queensland Museum's Digital Imaging Unit.

The shell sculpture of specimens was investigated and photographed using a TM-1000 Tabletop Scanning Electron Microscope located at the Queensland Museum. Shells were cleaned in an ultrasonic cleaner but not by chemical means in order to prevent the removal of the periostracum which maintains many of the shell's sculptural elements. Specimens were mounted on sticky tabs, gold sputter coated and imaged under high vacuum. Sculptural patterns of both the protoconch and teleoconch extensively examined. Protoconch were sculptural patterns were coded according to Holcroft (2018), viz. pitted cancellate (a lattice of broad spiral cords and radial ribs or ridges closely interwoven so that the distance between each is smaller than the width of the cord or rib resulting in a pitted appearance); superior **spiral** (spiral cords for only the first quarter

of a whorl followed by dominant spiral cords over raised radial ribs); **spiral** (spiral cords and no radial ribs); **early spiral** (spiral cords only for the first whorl followed by a pattern of strong radial ribs over the spiral cords for the remainder of the protoconch); **beaded cancellate** (thin interrupted spiral cords visible as round or elongate beads where they cross low radial ribs or ridges resulting in a beaded appearance).

Adult specimens of two species for which animal tissue was available, *Stanisicaropa chambersae* (Stanisic, 2010) comb. nov. and *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., were submerged in a shallow container of 75% ethanol and pinned to a black latex base using very fine 'Austerlitz' entomological pins. These pins were also used as dissection implements. Shells were removed and specimens were dissected. Photographs were taken of the male reproductive system using a NIKON Coolpix 4500 camera mounted on a WILD M5 stereo microscope. Photographs were labelled to show the internal anatomy of the penis which is considered to be species specific (Solem 1983).

A summary of specimens investigated by SEM and anatomical photography is included in Appendix 1.

RESULTS AND ANALYSIS.

Shell morphology. Mean shell measurements are shown in Table 1 and all specimens measured are tabulated in Appendix 1. Each species differed from all others in at least 10 conchological features with only 3 required to consider species differentiation. The only measurement that overlapped between species was the height/diameter ratio.

Scanning Electron Micrographs. SEM images showed four major protoconch sculptural patterns. A pitted cancellate protoconch is characteristic of *Biomphalopa* Stanisic, 1990 and *Stanisicaropa* gen. nov. (Figs 1B, C). All three forms of spiral protoconch sculpture were found *viz.* spiral, superior spiral and early spiral. Variations of a spiral protoconch were found on Amfractaropa gen. nov. and Comularopa gen. nov. (Figs 2A, B). Two slightly different superior spiral protoconchs were a feature of Whitcochlea gen. nov. and Xenoropa gen. nov. (Figs 2C, D). Radiolaropa gen. nov. and Nodularopa gen. nov. both shared an early spiral protoconch sculpture which showed variations in the number and prominence of the spiral cords and the nodulose pattern of the latter genus (Figs 1D, E, F). Genera sharing a particular protoconch sculpture were differentiated on the finer dimensions and characteristics of that sculpture together with other characteristics such as shell dimensions and anatomy. All MEQ Gyrocochlea-grade genera displayed a protoconch sculpture markedly different from the beaded cancellate pattern of Gyrocochlea s.s. (Fig. 1A).

Teleoconch microsculpture of the species exhibited both rounded ribbing on *Stanisicaropa chambersae* (predominately nodulose spiral cords over very fine radial threads) and *Biomphalopa recava* (radial threads over very fine spiral cords) and bladed ribbing in the other seven species (Fig. 3). The microsculpture of radial threads varied in number and size between species but was consistent within species including *Whitcochlea iuloidea* which occurs both on the mainland and on off-shore islands.

Anatomy. The terminal male genitalia of *Stanisicaropa chambersae* and *Whitcochlea iuloidea* were dissected (Figs 4A, B) and demonstrated two distinct penial configurations: *S. chambersae* with a pear-shaped penis lacking a penial sheath and lateral entrance of the epiphallus into the penial chamber (Fig. 5A); and *W. iuloidea* with a tubular-shaped penis with a penial sheath and apical entrance of the epiphallus into the penial chamber (Fig. 5B). Both species differed from the penial structure of *Biomphalopa recava* illustrated by Stanisic (1990).

SYSTEMATICS

ORDER EUPULMONATA

SUPERFAMILY PUNCTOIDEA

FAMILY CHAROPIDAE HUTTON, 1884

Biomphalopa Stanisic, 1990

Type species. *Endodonta recava* Hedley, 1912-by original designation.

Diagnosis. As cited in Stanisic (1990) with the re-description of the apical sculpture as pitted cancellate.

Remarks. *Biomphalopa* Stanisic, 1990 has a pitted protoconch sculpture (Fig. 2B) similar to that of *Stanisicaropa* gen. nov. (Fig. 2C) but differing in greater number of whorls and the

thickness of the radial ribs and spiral cords. The former is also distinguished from the latter genus by other aspects of shell morphology including the flammulated shell, bolder teleoconch ribbing and much wider, cup-shaped umbilicus. *Biomphalopa* differs from *Gyrocochlea* s.s. by having bolder protractively sinuated teleoconch ribs, a wider cup-shaped umbilicus and a coiling pattern that is multi-whorled in contrast to the nautiloid form of the latter. Stanisic (1990) also included *B. concinna* (Hedley, 1924) from the Wet Tropics, NEQ.

Biomphalopa recava (Hedley, 1912) (Figs 1B, 3A, 6A-B, 10, Table 1)

Endodonta recava Hedley, 1912: 267.

- Gyrocochlea recava (Hedley). Hedley, 1924: 217; Iredale, 1937; 323
- Biomphalopa recava (Hedley). Stanisic, 1990: 95. Smith, 1992: 182; Stanisic et al., 2010: sp. 389.



FIG. 1. Protoconch sculptures. **A**, Beaded cancellate: Type species of *Gyrocochlea* s.s., *Gyrocochlea* vinitincta (Cox, 1868), AMSC139752, Border Ranges, SEQ. **B-C**, Pitted cancellate: **B**, *Biomphalopa recava* (Hedley, 1912), QMMO85117, Finch Hatton Gorge, MEQ; C, Stanisicaropa chambersae (Stanisic, 2010) comb. nov., QMMO78961, Diggings Road, Eungella, MEQ. **D-F**, Early spiral: **D**, *Radiolaropa danieli* (Stanisic, 2010) comb. nov., QMMO35807, Endeavour Ck, MEQ. **E**, *Radiolaropa eungella* sp. nov., QMMO36099, Eungella Dam. **F**, *Nodularopa samanthae* sp. nov., QMMO77397, Upper Funnel Ck, MEQ. Scale bars = 100 m.

Material examined. Holotype. AMSC32992, Finch Hatton Gorge, 81 km W of Mackay, nvf under logs, coll. S. Jackson, 13.xii.1912.

Other material. Eungella: QMMO6345, 1SC; QMMO39878, 2RC; QMMO85176, 2SC; AMSC140230, 2RC; Broken R.: QMMO11715, 1RC. Diggings Road: QMMO11757, 1SC/2RC; QMMO13073, 2RC; Mt Dalrymple: QMMO36093, 1RC; QMMO6367, 1SC/1RC; QMMO77431, 3SC; QMMO85065, 1RC; Finch Hatton Gorge: QMMO11749, 1RC; AMSC153726, 1RC.

Distribution and habitat. Eungella NP, MEQ; in rainforest living under logs and other forest debris.

Remarks. *Biomphalopa recava* (Hedley, 1912) differs from all other MEQ *Gyrocochlea*-grade charopids by having a multi-whorled shell with a very wide cup-shaped umbilicus. The description detailed in Stanisic (1990) is adequate with the exception that the protoconch sculpture was described as 'regularly arranged pits and vague radial ridges' but is pitted cancellate in the new terminology proposed by Holcroft (2018). *B. recava* is a MEQ endemic species confined to the Clarke Ra. in the vicinity of Eungella NP and its environs.

Stanisicaropa gen. nov.

Type species. *Gyrocochlea chambersae* Stanisic, 2010-herein designated.

Etymology. For Dr John Stanisic in honour of his taxonomic work on Australian Charopidae; and a contraction of *Charopa*.

Diagnosis. Shell small, orange brown with darker radial bands, discoidal, nautiliform with a slightly sunken spire; protoconch pitted cancellate, pits formed by intersecting broad, low spiral cords and broad, low radial ridges of equal height; teleoconch with moderately spaced, broad, bold radial ribs and microsculpture of very crowded, very low microradial threads continuous on the major ribs and low microspiral cords forming beads at their intersection, spiral cords rolling over the major ribs; aperture ovately lunate; umbilicus wide cup-shaped; epiphallus long, entering penis laterally, penis pear-shaped with longitudinal pilasters. **Remarks**. *Stanisicaropa* gen. nov. differs from *Gyrocochlea* s.s. by having a pitted protoconch sculptural pattern (Fig. 1C) which contrasts markedly with the fine, beaded cancellate pattern seen in the latter (Fig. 1A). This difference is of similar magnitude to the differences between *Gyrocochlea* s.s. and some of the new genera of Shea *et al.* (2012) and is therefore considered sufficient justification for the description of a new genus to accommodate '*Gyrocochlea*' *chambersae* Stanisic, 2010. The genus appears to be endemic to MEQ (Stanisic, pers. comm.).

Stanisicaropa chambersae (Stanisic, 2010) comb. nov. (Figs 1C, 3B, 4A, 5A, 6C-D 10, Table 1)

Cyrocochlea chambersae Stanisic, 2010 (in Stanisic *et al.* 2010, sp. 295)

Material examined. Holotype. QMMO11758, Diggings Rd Eungella NP, 21°09′S, 148°29′E, nvf, coll., J. Stanisic, 8.vii.1982.

Paratypes. QMMO11714, 2SC/3RC, Eungella NP, Broken R., 21°10'S, 148°30'E, nvf, coll., J. Stanisic, 5.vii.1982; QMMO13071, 1RC, same data as holotype; QMMO13456, 1RC, Eungella NP, Broken R., 21°10'S, 148°30'E, nvf, coll., J. Stanisic, 5.vii.1982; QMMO50888,1RC, Eungella NP, Rocky Ck, 20°54'S, 148 35°E, coll., ANZES, 27.xii.1993; QMMO78961, 10SC, same data as holotype.

Other Material. Eungella NP: QMMO20224, 1SC; QMMO77427, 1SC; QMMO85102, 1RC; QMMO85113, 1SC; QMMO85118, 2SC; QMMO85119, 1SC; QMMO85120, 1SC; QMMO85121, 1SC; QMMO85122, 2SC; QMMO59648, 1RC; QMMO85174, 2SC. Broken R.: QMMO6375, 5SC; QMMO6377, 1SC; QMMO77435, 1SC. Pease's Lookout: QMMO85111, 1SC; QMMO85073, 1RC. Finch Hatton Gorge: QMMO85115, 1SC; Crediton Ck: QMMO6356, 2SC; QMMO85344, 3SC. Mt Macartney: QMMO35619, 1RC.

Diagnosis. As for genus.

Description. Shell small, orange brown with darker radial bands, discoidal, nautiliform with a slightly sunken spire; whorls 4.00-4.5 (mean 4.2); sutures moderately impressed; diameter of shell 3.5-4.4 mm (mean 3.99 mm), height 2.01 to 2.4 mm (mean 2.2 mm); H/D 0.51-0.61 (mean 0.55). Protoconch flat, 1.5 whorls, diameter 490-660 μ m (mean 550 μ m), pitted cancellate consisting of broad spiral cords and broad radial ridges, teleoconch with moderately

Taxon	n	D	Н	UW	AH	AW	PD	WWB	T1	H/D ratio	D/U ratio	No. whorls
Amfractaropa bretti	6	3.14	1.64	0.85	1.3	1.11	0.49	41	104	0.54	3.70	4.00
Biomphalopa recava	7	3.89	2.21	1.87	1.85	1.09	0.55	22	40	0.57	2.09	4.375
Comularopa georginae	1	2.30	1.31	0.66	0.90	0.66	0.41	66	132	0.57	3.50	3.875
Nodularopa samanthae	2	3.20	1.84	1.19	1.72	1.39	0.49	43	78	0.58	2.68	4.125
Radiolaropa danieli	3	3.17	1.80	1.26	1.50	1.17	0.49	42	79	0.61	2.57	3.75
Radiolaropa eungella	2	3.03	1.60	1.15	1.35	1.02	0.49	39	91	0.53	2.66	4.00
Stanisicaropa chambersae	13	5.04	2.78	1.65	2.11	1.65	0.55	20	53	0.55	3.08	4.25
Whitcochlea iuloidea	68	4.65	2.48	1.68	1.96	1.54	0.59	25	49	0.53	2.75	4.25
Xenoropa wigtonensis	2	6.02	2.87	2.01	2.09	2.01	0.78	52	67	0.48	3.00	4.375

TABLE 1. Mean shell measurements of MEQ Gyrocochlea-grade species examined in this study.



FIG. 2. Protoconch sculptures. **A-B**, Spiral: A, *Amfractaropa bretti* sp. nov., QMMO11716, Broken R., MEQ; **B**, *Comularopa georginae* sp. nov., QMMO59645, Crediton Ck, MEQ. **C-D**, Superior spiral: **C**, *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., QMMO6342, Brandy Ck, Conway Ra., MEQ. **D**, *Xenoropa wigtonensis* sp. nov., QMMO85180, Wigton I., MEQ. Scale bars = 100 m.





FIG. 3. Teleoconch sculpture. **A**, *Biomphalopa recava* (Hedley, 1912), QMMO39878, Finch Hatton Gorge, MEQ. **B**, *Stanisicaropa chambersae* comb. nov., QMMO78961, Eungella, MEQ. C, *Radiolaropa danieli* (Stanisic, 2010) comb. nov., QMMO35807, Endeavour Ck, MEQ. **D**, *Radiolaropa eungella* sp. nov., QMMO36099, Eungella Dam. **E**, *Nodularopa samanthae* sp. nov., QMMO77397, Upper Funnel Ck, MEQ. **F**, *Amfractaropa bretti* sp. nov., QMMO11716, Broken R., MEQ. **G**, *Comularopa georginae* sp. nov., QMMO59546, Crediton Ck, MEQ; **H**, *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., QMMO85334, Brandy Ck, Conway Ra., MEQ. **I**, *Xenoropa wigtonensis* sp. nov., QMMO70431, Wigton I., MEQ. All magnification 600X.

spaced, bold radial ribs, 42-61 (mean 53) on the first whorl; microsculpture of extremely fine microradial threads and low, spiral cords forming beads at their intersections with the microradials, rolling unbroken over the major teleoconch ribs; aperture ovately lunate; umbilicus wide cup-shaped, diameter 1.00-1.46 mm (mean 1.3 mm), DU 2.6-3.7 (mean 3.08). Based on 13 measured adult specimens.

Terminal male genitalia (Figs 4A, 5A). Vas deferens-epiphallus junction a ball and socket arrangement; epiphallus long, longer than penis, initially swollen becoming thinner approaching the penis, bound to penis head in the vicinity of the penial retractor muscle attachment, before descending and entering penis laterally through a simple pore with a muscular collar. Penis pearshaped, internally with longitudinal pilasters; length 1.69 mm. Based on one dissected specimen (QMMO78961).

Distribution and habitat. Eungella to Mt Macartney. Clarke Ra., MEQ, in moist humid rainforest living under logs.

Remarks. Stanisicaropa chambersae (Stanisic, 2010) comb. nov. can be readily distinguished from other MEQ Gyrocochlea-grade species by the combination of pitted cancellate protoconch and more intense microradial ribbing rolling over the major ribs on the teleoconch (Figs 1C, 3B). The protoconch pattern in *S. chambersae* is broadly similar to that of *Biomphalopa recava* (Hedley, 1912) in that it is pitted cancellate. However, B. recava has a pitted cancellate sculpture with narrow spiral cords and wider radial ribbing compared to that of S. chambersae which has much broader spiral cords (Figs 1B, C). The orange-brown coloured shell with slightly sunken spire, open cup-shaped umbilicus and nautiloid coiling of S. chambersae also differs from that of *B*. recava which has a cream coloured shell with reddish-brown flammulations and a strongly biconcave, multi-whorled shell with a wide cup-shaped umbilicus. S. chambersae has a long epiphallus entering the pear-shaped penis laterally (Fig. 4A) similar to that of B. recava which has a the tubular penis and much shorter epiphallus (Stanisic 2010: Fig. 58b). S. *chambersae* is restricted to the moist rainforests

of Eungella NP in the Clarke Ra. With an annual rainfall of around 2300 mm (Bureau of Meteorology 2017), the Eungella Plateau rises to an altitude of 1259 m at Mt Dalrymple. The species has been collected from lower altitudes at Broken R. (alt. 470 m) and Finch Hatton Gorge (alt. 250 m) to the higher slopes of Mt Dalrymple.

Radiolaropa gen. nov.

Type species. *Gyrocochlea danieli* Stanisic, 2010-herein designated.

Etymology. From the Latin *radiolus* = rays referring to the 'dominant radial ribs on the protoconch.'

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; whorls rounded, last weakly descending; protoconch early spiral with prominent, curved radial ribs and very low spiral cords (Fig. 1D); teleoconch with very crowded, bladed radial ribs (c. 150 on last whorl), microsculpture of prominent microradial threads over very low microspiral cords forming weak buttresses at their intersection with the microradials; umbilicus wide, V-shaped.

Remarks. Radiolaropa gen. nov. differs from both Whitcochlea gen. nov. and Stanisicaropa gen. nov. by the combination of smaller size, having more prominent radial ribs on the early spiral protoconch and in having a much more densely ribbed teleoconch. Radiolaropa differs from *Gyrocochlea* s.s. by having an early spiral protoconch (Fig. 1D) which contrasts with the fine, beaded cancellate pattern seen in the latter (Fig. 1A). This difference is equivalent to the differences between *Gyrocochlea s.s.* and some of the new genera described by Shea et al. (2012) and is herein considered sufficient to justify the description of a new genus for 'Gyrocochlea' danieli Stanisic, 2010 with the addition of R. eungella sp. nov. Further Radiolaropa species may be present in the Rockhampton-Byfield area, SEQ (Stanisic, pers. comm).

Radiolaropa danieli (Stanisic, 2010) comb. nov. (Figs 1D, 3I, 7A-B, 10, Table 1)

Gyrocochlea danieli Stanisic, 2010 (in Stanisic *et al.* 2010, sp. 294).

Material examined. Holotype. QMMO35807, 1RC, upper reaches of Endeavour Ck, Clarke Ra., W of Mackay, 21°15′30″S, 148°37′30″E, rainforest, under logs, coll. J. Stanisic, 20.v.1990.

Paratypes. QMMO11745, 4SC, same data as holotype.

Other material. QMMO85340, 1RC, Cherry Tree Ck, 1.2 km off Pinnacle Station Road, MEQ, vine forest, 21° 12' S, 148° 42' E, under rocks and logs, coll., J. Stanisic, L. Holcroft, 17.xi.2016.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; whorls rounded, last weakly descending; protoconch early spiral with very low spiral cords and prominent, radial ribs (Fig. 1D); teleoconch with very crowded, bladed radial ribs (c. 150 on last whorl), microsculpture of prominent microradial threads over very low microspiral cords forming weak buttresses at their intersection with the microradials; umbilicus wide, V-shaped.

Description. Shell tiny, orange-brown with darker radial bands, discoidal, nautiliform with a slightly sunken spire; whorls 4.125; sutures moderately impressed; diameter of shell 2.92 mm, height 1.62 mm; H/D 0.5-0.66 (mean 0.61). Protoconch flat, 1.5 whorls, diameter 490 µm, early spiral with low spiral cords and widely spaced prominent, radial ribs on the latter part of the protoconch; teleoconch with crowded radial ribs, 67-94 (mean 79) on the first whorl; microsculpture of microradial threads and very low spiral cords buttressing against the radial threads; aperture ovately lunate; umbilicus wide, V-shaped, diameter 1.07-1.56 mm (mean 1.26mm), D/U 1.84-3.46 (mean 2.57). Based on 3 measured adult specimens.

Distribution and habitat. Endeavour Ck and Cherry Tree Ck, Clarke Ra., MEQ; restricted to riparian rainforest environments of Endeavour Ck and Cherry Tree Ck south of Finch Hatton, living under logs and rocks.

Remarks. *Radiolaropa danieli* (Stanisic 2010) comb. nov. is distinguished by the combination of strong bladed, radial ribs on the early spiral

protoconch which run over the spirals and more intense teleoconch ribbing (Figs 1D, 3C). A specimen from Bell's Gap (QMMO11745) was originally considered conspecific with *R. danieli* by Stanisic *et al.* (2010) but is shown to be a different species below. *R. danieli* is found at Endeavour Ck and Cherry Tree Ck in the lower altitudes of the Crediton SF, MEQ (alt. 575 m). Both creeks are relatively inaccessible and further collecting of the surrounding habitats is needed to establish the full extent of the species' range.

Radiolaropa eungella **sp. nov.** (Figs 1E, 3D, 7C-D, 10, Table 1)

Etymology. Named for the Eungella Dam area, the type locality.

Preferred common name. Eungella Dam Pinwheel Snail

Material examined. Holotype. QMMO36099, 1RC, Eungella Dam, c. 1.5 km E on road to Eungella, W Mackay, 21°10'S, 148°23'E, coll. J. Stanisic, 21.v.1990. Diameter 2.95 mm, height 1.56 mm, H/D 0.53, D/U 2.4, number of whorls 4.125.

Paratype. QMMO85343, 1RC, Hazelwood Ck, Lizzie Ck Rd at pipeline Xing, MEQ, sevt, 20° 10' S, 148° 22' E, under rocks, coll. J. Stanisic, L. Holcroft, 18.xi.2016.

Other Material. AMSC154898. 1RC, Homevale, N of Nebo, 21° 24' S, 148° 33' E, 440m, sevt, coll. J. Burch, W. Ponder, P. Colman, 5.v.1975.

Diagnosis. Shell tiny, white, discoidal, nautiliform with a slightly sunken spire; protoconch early spiral with initial low, broad spiral cords rising over strong, bold radial ribs after the first whorl; teleoconch with very crowded, moderately thin, bladed radial ribs recurved towards the suture at the apical end and microsculpture of prominent microradial threads and low microspiral cords forming buttresses at their intersection with the microradials; umbilicus V-shaped.

Description. Shell tiny, white, discoidal, nautiliform with a slightly sunken spire; whorls 3.875-4.125 (mean 4); sutures moderately impressed; diameter of shell 2.95-3.11 mm (mean 3.03 mm), height 1.56-1.64 mm (mean 1.6 mm); H/D 0.53. Protoconch flat, 1.5 whorls, diameter 490 µm, early spiral with initial low,



FIG. 4. Terminal male genitalia. A, *Stanisicaropa chambersae* (Stanisic, 2010) comb. nov., QMMO78961. B, *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., QMMO85338. Scale bars = 1 mm.



FIG. 5. Internal penial anatomy. **A**, *Stanisicaropa chambersae* (Stanisic, 2010) comb. nov., QMMO78961. **B**, *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., QMMO85338. Scale bars = 1 mm.

Holcroft, L.



FIG. 6. Dorsal and ventral views of shells. **A-B**, *Biomphalopa recava* (Hedley, 1912), QMMO39878, paratype, Finch Hatton Gorge, MEQ. **C-D**, *Stanisicaropa chambersae* (Stanisic, 2010) comb. nov., QMMO11758, holotype, Eungella, MEQ. Images: Geoff Thompson, QM.

broad spiral cords rising over strong, bold, radial ribs after the first whorl; teleoconch with very crowded, radial ribs 86-95 (mean 91 on the first whorl), prominent microradial threads and low microspiral cords forming buttresses at their intersection with the microradials; aperture ovately lunate; umbilicus V-shaped, diameter 1.07-1.23 mm (mean 1.15 mm), D/U 2.40-2.92 (mean 2.6). Based on 2 measured adult specimens.

Distribution and habitat. Eungella Dam area, Hazelwood Gorge, Homevale, MEQ; in semievergreen vine thicket living under logs and rocks.



FIG. 7. **A-B**, *Radiolaropa danieli* (Stanisic, 2010) comb. nov., QMMO35807, holotype. Endeavour Ck, MEQ. C-D, *Radiolaropa eungella* sp. nov., QMMO36099, holotype, Eungella Dam, MEQ. E-F, *Nodularopa samanthae* sp. nov., QMMO77397, holotype, Upper Funnel Ck, MEQ. Images: Geoff Thompson, QM.

Remarks. *Radiolaropa eungella* sp. nov. can be separated from *R. danieli* (Stanisic, 2010) comb. nov. by the white shell colour, lower H/D ratio, finer teleoconch ribbing and smaller umbilical width. *R. eungella* with the preferred habitat of semi-evergreen vine thickets of Eungella Dam, Hazelwood Gorge and Homevale, MEQ, shares similar shell dimensions and protoconch sculpture to those of *Nodularopa samanthae* sp. nov. from moister rainforests of the eastern escarpments of the Connors Ra. closer to the MEQ coast, but can be distinguished by the combination of lighter shell colour and lack of nodulose protoconch and teleoconch sculpture.

Nodularopa gen. nov.

Type species. *Nodularopa samanthae* sp. nov.- herein designated.

Etymology. From the Latin *nodulus* = a small, knot like protuberance, relating to the nodular appearance of the radial ribs on both the protoconch and teleoconch; and a contraction of *Charopa*.

Diagnosis. Shell tiny, white to brown, discoidal, nautiliform with a slightly sunken spire; protoconch early spiral with initial low, broad spiral cords rising over strong, bold radial ribs forming nodules at their intersection; teleoconch with crowded radial ribs crossed by low microspiral cords forming nodules at their intersection; microsculpture of prominent microspiral cords and thin microradial threads forming beads or nodules at their intersection; umbilicus wide, V-shaped.

Remarks. *Nodularopa* gen. nov. is distinguished from other MEQ *Gyrocochlea*-grade genera by the combination of a nodulose early spiral protoconch and nodulose radial ribbing on the teleoconch. Additional *Gyrocochlea*-grade species possessing similar nodulose shell sculpture exist in the Calliope-Rockhampton area, SEQ but require further study in order to confirm their inclusion in *Nodularopa* (Stanisic, pers. comm.).

Nodularopa samanthae sp. nov. (Figs 1F, 3E, 7E-F, 12, Table 1)

Gyrocochlea danieli Stanisic 2010 (in Stanisic et al. 2010) [partim] **Etymology.** Named for the author's daughter, Samantha.

Preferred common name. Nodular Pinwheel Snail

Material examined. Holotype. QMMO77397, 1RC, Sarina, SW at upper Funnel Ck, 21°34'S, 149°12'E, 200-450m, coll. QM party, 16.xi.1992. Diameter 2.79 mm, height 1.64 mm, H/D 0.59, D/U 2.62, number of whorls 4.

Other material. QMMO11745, 1RC; QMMO13081, 3RC, Bell's Gap, Sarina Ra., c. 15km S Sarina on Bruce Highway, 21°31'S, 149°07'E, coll. J. Stanisic, 7.vii.1982.

Diagnosis. As for genus.

Description. Shell tiny, brown, discoidal, nautiliform with a slightly sunken spire; whorls 4-4.25 (mean 4.125); sutures moderately impressed; diameter of shell 2.79-3.61 mm (mean 3.2 mm), height 1.64-2.05 mm (mean 1.84 mm); H/D 0.57-0.59 (mean 0.58). Protoconch flat, 1.5 whorls, diameter 490 µm, early spiral with initial low, broad spiral cords rising over strong, bold, radial ribs after 1 whorl creating nodules at their intersection; teleoconch with very crowded, nodulose radial ribs 60-95 (mean 78) on the first whorl, microsculpture of crowded and prominent microspiral cords and crowded, thin microradial threads forming beads or nodules at their intersection; aperture ovately lunate; umbilicus wide, V-shaped, diameter 1.07-1.31 mm (mean 1.19 mm), D/U 2.62-2.75 (mean 2.68). Based on 2 measured adult specimens.

Distribution and habitat. Funnel Ck and Bell's Gap, Connors Ra., MEQ; in moist humid rainforest living under logs.

Remarks. *Nodularopa samanthae* sp. nov. can be readily distinguished by the nodulose early spiral protoconch sculpture and prominent nodulose teleoconch ribbing (Figs 3F, 4H). The specimens from Funnel Ck were previously undescribed while the specimens from Bell's Gap were originally ascribed to 'Gyrocochlea' danieli Stanisic, 2010 (Stanisic et al. 2010) based on gross shell similarity. More detailed study by SEM has shown that there is a marked difference in early the spiral protoconch sculpture between the latter species and *N. samanthae* having closely spaced spiral cords that form a nodule at the intersection of the radial ribs in the second part of the protoconch unlike that of both *Radiolaropa* gen. nov. species where the weak spiral cords run under the stronger, more prominent radial ribs. This warrants both specific and generic separation.

Amfractaropa gen. nov.

Type species. Amfractaropa bretti sp. nov.- herein designated.

Etymology. From the Latin *amfractus* = coil or spiral relating to the protoconch sculptural pattern; and a contraction of *Charopa*.

Diagnosis. Shell tiny, brown, discoidal, nautiliform with a slightly sunken spire; protoconch flat, 1.75 whorls, spiral with broad spiral cords and broad radial ridges only appearing after 1.5 whorls - in a transition to the teleoconch that occupies ¼ of a whorl; teleoconch with very crowded radial ribs, microsculpture of prominent microradial threads and numerous, low microspiral cords forming buttresses at their intersection with the microradials, spiral cords rolling over the major ribs, though ribs appearing as blades where the shell has been worn; umbilicus wide V-shaped.

Remarks. *Amfractaropa* gen. nov. can be distinguished from other MEQ Gyrocochleagrade genera by the combination of brown shell colour, spiral protoconch sculpture, a longer than normal protoconch (1.5 whorls), dense radial ribbing on the teleoconch and a wide V-shaped umbilicus. Amfractaropa is similar to Diphyoropa Hyman & Stanisic, 2005 from SEQ and NSW in having similar shell sculpture and a longer than normal spiral protoconch with the last quarter whorl transitioning into the teleoconch having broad radial ribs. However, Amfractaropa can be distinguished from Diphyoropa by having a protoconch sculpture of regular spiral cords unlike the bimodal spiral pattern of Diphyoropa. Several undescribed species with a similar protoconch sculpture from the SEQ may also belong in Amfractaropa (Holcroft, unpub.). The species is found in the rainforest of the Broken R. in the Eungella NP, MEO.

Amfractaropa bretti sp. nov. (Figs 2A, 3F, 8A-B, 10, Table 1)

Etymology. Named for the author's son, Brett.

Preferred common name. Broken River Pinwheel Snail

Material examined. Holotype. QMMO6376, 1RC, Eungella NP, Broken R, 21°10′S, 148°30′E, 800m, coll., M. Bishop, xi.1976. Diameter 3.2 mm, height 1.64 mm, H/D 0.51, D/U 5.57, number of whorls 4.125.

Paratypes. QMMO11716, 3SC, Eungella NP, Broken R, 21°10′S, 148°30′E, nvf, coll., J. Stanisic, 5.vii.1982.

Other material. QMMO59545, 1SC, Crediton Ck, Eungella NP, 21°11′S, 148°32′E, 850m, coll., M. Bishop, xi.1976.

Diagnosis. As for genus.

Description. Shell tiny, brown, discoidal, nautiliform with a slightly sunken spire; whorls 4; sutures moderately impressed; diameter of shell 2.87-3.52 mm (mean 3.14 mm), height 1.39-1.8 mm (mean 1.61 mm); H/D 0.47-0.54 (mean 0.51). Protoconch flat, 1.75 whorls, diameter 490 µm, spiral with broad spiral cords, and broad radial ridges only appearing after 1.5 whorls in a transition to the teleoconch; teleoconch with very crowded radial ribs, 83-121 (mean 104) on the first whorl; microsculpture of prominent microradial threads and numerous, low microspiral cords forming buttresses at their intersection with the microradials, spiral cords rolling over the major ribs though ribs appearing as blades where the shell has been worn; aperture ovately lunate; umbilicus wide V-shaped, diameter 0.57-1.07 mm (mean 0.85 mm), D/U 3-5.57 (mean 3.94). Based on 6 measured adult specimens.

Distribution and habitat. Broken R. and catchment area, Eungella NP, MEQ; in moist humid rainforest living under logs.

Remarks. Amfractaropa bretti sp. nov. is distinguished among MEQ Gyrocochleagrade charopids by having a spiral protoconch with broad spiral cords (Fig. 3A). However, *Diphyoropa jonesi* Stanisic, 2010 from Goomeri, SEQ and several undescribed species from SEQ (Bunya Mts, Mt Mudlo and Gatton) have a comparable spiral sculpture on a longer than normal protoconch and similar teleoconch structures (Holcroft, pers. obs.). However, *A. bretti* differs from these southern species by having a larger number of broader spirals on the protoconch especially towards the suture (mean 19). Further investigation of possible links with the SEQ charopids with the similar protoconch architecture is needed to confirm possible relationships. The longer protoconch length of 1.75 whorls separates *A. bretti* from two other MEQ charopid species with spiral protoconchs viz. *Comularopa georginae* sp. nov. and *Sinployea intensa* (Iredale, 1941) (see Stanisic 1990), both of which have the more common protoconch of 1.5 whorls.

Comularopa gen. nov.

Type species. *Comularopa georginae* sp. nov.- herein designated.

Etymology. From the Latin *comula* = dainty; and a contraction of *Charopa*.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; protoconch spiral with thin spiral cords; teleoconch with extremely crowded radial ribs, microsculpture of prominent microradial threads and numerous, low microspiral cords forming buttresses at their intersection with the microradials, spiral cords rolling over the major ribs; umbilicus wide V-shaped.

Remarks. *Comularopa* gen. nov. is distinguished from other MEQ Gyrocochlea-grade genera by the combination of light brown shell colour, protoconch sculpture of thin spiral cords, ultra-fine radial ribbing on the teleoconch and a narrow, U-shaped umbilicus. Comularopa is similar to Amfractaropa gen. nov. in shell sculpture but can be distinguished from the latter by having smaller shell dimensions but most notably, a smaller protoconch diameter (Table 1). The protoconch sculpture of *Comularopa* consists of thin, continuous equally spaced spiral cords running all the way to the teleoconch. As such, there is no transition zone of different microsculpture before the beginning of the teleoconch, in contrast to the case in larger charopids including *Amfractaropa*. Although the genus is currently considered monotypic

additional species of *Comularopa* may occur in the Rockhampton-Byfield area, SEQ (Stanisic, pers. comm.).

Comularopa georginae. sp. nov. (Figs 2B, 3G, 8C-D, 10, Table 1)

Etymology. Named for the author's daughter-in-law, Georgina.

Preferred common name. Crediton Creek Pinwheel Snail

Material examined. Holotype. QMMO59546, 1RC, Crediton Ck, Eungella NP, 21°11′S, 148°32′E, 850 m, coll., M. Bishop, xi.1976. Diameter of shell 2.3 mm, height 1.31 mm, H/D 0.57, D/U 3.5, number of whorls 3.875.

Paratypes. QMMO59645, 2RC, same data as holotype.

Description. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; whorls 3.875; sutures moderately impressed; diameter of shell 2.3 mm, height 1.31 mm; H/D 0.57. Protoconch flat, 1.5 whorls, diameter 410 μ m, spiral with thin, bladed equidistant spiral cords (mean 13), teleoconch with ultra-fine crowded radial ribs, 132 on the first whorl; microsculpture of prominent microradial threads and numerous, low microspiral cords forming buttresses at their intersection with the microradials, spiral cords rolling over the major ribs; aperture ovately lunate; umbilicus wide V-shaped, diameter 0.66 mm, D/U 3.5. Based on 1 measured adult specimen.

Distribution and habitat. Hitherto known only from Crediton Ck, Eungella NP, MEQ; in moist humid rainforest living under logs.

Remarks. *Comularopa georginae* sp. nov. can immediately distinguished by the spiral protoconch consisting of thin bladed, equidistant spirals (Fig. 3B) and also differentiates the species from the grossly similar *Amfractaropa bretti* sp. nov. which has a spiral protoconch with low, broad spirals. In addition *C. georginae* has a smaller protoconch diameter (consistently larger in *A. bretti*, Table 1) and a lower D/U ratio. While it may seem ambitious to describe a genus and species on a single adult specimen, the distinctive spiral protoconch is thus far unique among eastern Australian *Gyrocochlea*-



FIG. 8. Dorsal and ventral views of shells. **A-B**, *Amfractaropa bretti* sp. nov., QMMO6376, holotype, Broken R., MEQ. **C-D**, *Comularopa georginae* sp. nov., QMMO59546, holotype, Crediton Ck, MEQ. Images: Geoff Thompson, QM.

grade species and is considered justification for such a decision.

Whitcochlea gen. nov.

Type species. *Helix iuloidea* Forbes, 1851-herein designated.

Etymology. From a contraction of Whitsunday and a contraction of *Gyrocochlea*, alluding to the distribution of the species in the Whitsunday biogeographic province and the general similarity to *Gyrocochlea* s.s.

Diagnosis. Shell small, brown, discoidal, nautiliform with a slightly sunken spire;

protoconch superior spiral with numerous, low, broad spiral cords becoming thinner towards the protoconch-teleoconch boundary rising over low curved radial ridges; teleoconch with crowded, moderately thin, bladed radial ribs recurved towards the suture at the apical end and microsculpture of prominent microradial threads and low microspiral cords forming buttresses at their intersection with the microradials; umbilicus wide, cup-shaped; penis tubular with longitudinal pilasters and a long epiphallus entering the penis apically. **Remarks**. *Whitcochlea* gen. nov. can be distinguished from other MEQ *Gyrocochlea*-grade genera by the combination of a relatively large-sized, brown shell, superior spiral protoconch sculpture, dense radial ribbing on the teleoconch and a very wide umbilicus. The genus appears to be monotypic and endemic to MEQ.

Whitcochlea iuloidea (Forbes, 1851) comb. nov. (Figs 2C, 3H, 4B, 5B, 9A-B, 10, Table 1)

Helix iuloidea Forbes, 1851: 379.

Gyrocochlea iuloidea (Forbes). Iredale, 1937: 323; Smith, 1992: 191; Stanisic, 2010 (in Stanisic *et al*. 2010, sp. 296)

Syntypes. NHM1859.3.11.15, 2 specimens (*fide* Smith 1992), Port Molle, MEQ-therein designated.

Taxonomic issues. The syntypes cited in Smith (1992) were not sighted and unable to be located by staff of the NHM, London. Topotypic specimens were collected and used in this study.

Material examined. Long I: QMMO64881, 1SC/1RC; QMMO64807, 45C/3RC; QMMO74082, 15C/6RC; QMMO85338, 65C/7RC. Conway Ra.: QMMO85181, 1RC; QMMO6342, 28RC; JW1449, 2RC; QMMO6340, 13SC; QMMO6341, 2RC; QMMO6343, 1SC; QMMO19928, 7SC; QMMO35366, 3SC; QMMO59185, 1SC; QMMO85110, 16SC; QMMO85124, 1RC; AMSC154888, 6RC; AMSC154889, 1RC; QMMO85334, 8SC/6RC. Riordan Vale: JW1512, 11RC. Airlie Beach: QMMO20143, 4RC/2SC; QMMO35357, 4SC/8RC. Ĝloucester I: QMMÓ85186, ÎRC; QMMÓ74108, 1RC. Hamilton I: QMMO85182, 1RC; QMMO65833, 2RC. Peter Faust Dam: QMMO85183, 1RC; QMMO35569, Whitsunday I: OMMO85184, 2SC/5RC. 1RC; 2SC/2RC. 4RC; QMMO65923, QMM065943, Proserpine R: QMMO85185, 1RC; QMMO39879, 2RC; JW3857, 2RC; QMMO42391, 1RC; QMMO58018, 2SC/1RC; QMMO77414, 3SC; QMMO77418, 1SC; QMMO85107, 1SC. Mt Dryander: QMMO85187, 1RC; QMMO35545, 12SC; JW3433, 8RC; QMMO19981, 15SC/5RC; QMMO35560, 6SC/2RC; QMMO54774, 1RC; QMM059193, 6SC; QMM077221, 1SC; QMM077444, 3SC; AMSC140445, 4RC; AMSC154894, 1RC. Mt Jukes: JW3444, 3RC.

Diagnosis. As for genus.

Description. Shell small, brown, discoidal, nautiliform with a slightly sunken spire; whorls 4-4.75 (mean 4.25); sutures moderately impressed; diameter of shell 3.61- 5.66 mm (mean 4.66 mm), height 1.8-3.11 mm (mean 2.48 mm); H/D 0.33-0.72 (mean 0.53). Protoconch flat, 1.5 whorls, diameter 490-740 μ m (mean 610 μ m), superior spiral with low, broad spiral

bands over weaker radial ribs; teleoconch with crowded radial ribs, 43-66 (mean 48) on the first whorl; microsculpture of microradial threads and very low spiral cords buttressing against the radial threads; aperture ovately lunate; umbilicus wide cup-shaped, diameter 1.39-2.03 mm (mean 1.68 mm), D/U 2.5-3 (mean 2. 75). Based on 68 adult specimens.

Terminal male genitalia (Figs 4B, 5B). Vas deferens-epiphallus junction, a ball and socket arrangement; epiphallus long, longer than penis, initially swollen but becoming thinner nearing penis, entering penis apically through a simple pore. Penis tubular with a thin penial sheath; internally with longitudinal pilasters; penial retractor muscle inserting apically on penis head; length 1.43mm. Based on 1 dissected specimen.

Distribution and habitat. Proserpine R. environs, Mt Dryander, Conway Ra., Gloucester I. and the Whitsunday islands, MEQ; in drier araucarian rainforest living under logs and rocks.

Remarks. Whitcochlea iuloidea (Forbes, 1851) comb. nov. was described from Port Molle (= Long I.), MEQ, but the syntypes could not be located in the Natural History Museum, London. As a result, the concept of the species adopted here is based on previous records and other material collected since 1980 and in particular, specimens collected on a 2016 field trip to the type locality. W. iuliodea has a superior spiral protoconch (Fig. 3C) which differs from all other known MEQ charopids with the exception of *Xenoropa wigtonensis* sp. nov. and can be distinguished from that species by its smaller size, wider teleoconch ribbing and by broader spiral cords on the protoconch. W. *iuloidea* is found in the Whitsunday biogeographic province which includes the araucarian rainforests of the Whitsunday islands, the Conway Ra., Mt Dryander and the riparian rainforest along the Proserpine R. These drier coastal rainforests, which receive an annual average rainfall of 1300 mm (Bureau of Meteorology 2017), harbour this single *Gyrocochlea*-grade species which is characterised by a superior spiral protoconch. Specimens from Long I. and Mt Dryander



FIG. 9. Dorsal and ventral views of shells. **A-B**, *Whitcochlea iuloidea* (Forbes, 1851) comb. nov., QMMO64881, topotype, Long I, MEQ. **C-D**, *Xenoropa wigtonensis* sp. nov., QMMO85180, holotype, Wigton I, MEQ. Images: Geoff Thompson, QM.

have slightly larger shells than those from the Conway Ra., Mt Jukes and the Proserpine R. (Table 1) although all have a similar shell colour and identical teleoconch sculpture. The specimens group into a single species showing links from the time when sea levels were lower and the land masses connected approximately 15 000 years ago (Willmott 2006).

Xenoropa gen. nov.

Type species. Xenoropa wigtonensis -herein designated.

Etymology. From the Ancient Greek *xeno* = foreign relating to granitic xenolithic rock formations found in the South Cumberland Islands; and a contraction of *Charopa*.

Diagnosis. Shell small, orange brown with darker radial bands, discoidal, nautiliform with

a slightly sunken spire; protoconch superior radial with narrow, bladed spiral cords and weaker raised radial ribs, teleoconch with crowded radial ribs and microsculpture of microradial threads and low spiral cords buttressing against the radial threads; aperture ovately lunate; umbilicus wide cup-shaped.

Remarks. *Xenoropa* gen. nov. has a similar superior spiral protoconch sculpture to *Whitcochlea* gen. nov. but is distinguished by having more defined and raised spiral cords and raised radial ribbing on the protoconch as well as by its larger shell dimensions (diameter, height and protoconch diameter, see Table 1). *Xenoropa* gen. nov. is only known from Wigton I., MEQ, however, it may well have a wider distribution on the adjacent mainland.

Xenoropa wigtonensis **sp. nov.** (Figs 2D, 3I, 9C-D, 10, Table 1)

Etymology. For Wigton I., the type locality.

Preferred common name. Wigton Island Pinwheel Snail.

Material examined. Holotype. QMMO85180, 1RC, Wigton I., NE of Mackay, 20° 43' 25" S, 149° 27' 36" E, coll., J. Stanisic, T. Carless, 21.viii.2001. Diameter of shell 6.15 mm, height 2.95 mm, H/D 0.48, D/U 3.23, number of whorls 4.375.

Paratype. QMMO70431, 1RC, same data as holotype.

Diagnosis. As for genus.

Description. Shell small, brown, discoidal, nautiliform with a slightly sunken spire; whorls 4.375; sutures moderately impressed; diameter of shell 5.9-6.15 mm (mean 6.02 mm), height 2.79-2.95 mm (mean 2.87 mm); H/D 0.47-0.48 (mean 0.48). Protoconch flat, 1.5 whorls, diameter 740-820 µm (mean 780 µm), superior spiral with narrow, bladed spiral bands over weaker raised radial ribs, teleoconch with crowded radial ribs, 57-68 (mean 68) on the first whorl; microsculpture of microradial threads and very low spiral cords buttressing against the radial threads; aperture ovately lunate; umbilicus wide cup-shaped, diameter 1.97-2.05 mm (mean 2.01 mm), D/U 2.88-3.13 (mean 3). Based on 2 measured adult specimens.

Distribution and habitat. Hitherto known only from Wigton I., MEQ; in araucarian rainforest living under logs.

Remarks. Xenoropa wigtonensis sp. nov. is broadly similar to Whitcochlea iuloidea (Forbes, 1851) in having a brown shell with similar umbilical width and apertural height and a superior spiral protoconch sculpture (Fig. 2D). However, X. wigtonensis is distinguished from *W. iuloidea* by the combination of a larger shell diameter (over 6 mm) and shell height, a larger number of whorls, a larger protoconch diameter and much denser radial ribbing on the teleoconch (mean 52 ribs on the third quarter of body whorl as opposed to an average of 25 on the third quarter of the body whorl of *W*. iuloidea: Table 1). No animal tissue of this species was available for anatomical analysis and the description was made from two worn specimens. The SEM image of the protoconch sculpture was taken through the umbilicus due to damage on the apices of each specimen. Additional material is needed to more fully document the species conchological features.

X. wigtonensis is presently known only from Wigton I. in the south Cumberland Group and not from the Whitsunday Islands. However, further collecting on this and the surrounding islands may extend the range of this species. W. iuloidea, first recorded from an off-lying island was subsequently found on the adjacent mainland areas and given the similar geological history of this region, it is quite possible for X. wigtonensis or a sister species to be present on the adjacent mainland. However, given that this section of the mainland is part of the Proserpine-Sarina lowlands that have been heavily impacted by clearing for sugar cane farming and cattle grazing, a continental relative in mainland MEQ could be difficult if not impossible to locate. Continental relatives may be present on the mainland further south.

Discussion. *Gyrocochlea* Hedley,1924 has historically been a convenient generic 'repository' for eastern Australian mainland charopids with prominently ribbed, brown discoidal shells. Shea *et al.* (2012) have shown that *Gyrocochlea* s.s. only applies to a small suite



FIG. 10. Map showing localities of MEQ Gyrocochlea-grade species. Species are identified by the following symbols: ♦ *Biomphalopa recava* (Hedley, 1912); ▲ *Stanisicaropa chambersae* (Stanisic, 2010) comb. nov.; ● *Radiolaropa danieli* (Stanisic, 2010) comb. nov.; ◆ *Radiolaropa eungella* sp. nov.; ■ *Amfractaropa bretti* sp. nov.; ● *Comularopa georginae* sp. nov.; ★ *Whitcochlea iuloidea* (Forbes, 1851) comb. nov.; ▼ *Xenoropa wigtonensis* sp. nov.; ₩ *Nodularopa samanthae* sp. nov.

of species in SEQ and NENSW and that the historical generic concept was polyphyletic and concealed a vast hidden diversity of charopid evolution. Only four species of *Gyrocochlea*-grade charopids have been previously described from MEQ and the present study has shown that a similar scenario exists with these species. The consequent necessary reassignment of these species and the description of new species of *Gyrocochlea*-grade charopids from MEQ in this study has led to the description of seven new genera largely based on differences in protoconch sculpture.

All new genera in this paper can be recognised using protoconch sculpture which differs markedly from the beaded cancellate pattern of true *Gyrocochlea s.s.* (Fig. 1A). Investigations under optical microscopy reveal a predominantly spiral pattern on most protoconchs. Closer examination under SEM (Figs 1, 2) provides further differentiation in the spiral pattern with superior spiral (*Whitcochlea* and *Xenoropa*), spiral (*Amfractaropa* and *Comularopa*), early spiral (*Nodularopa* and *Radiolaropa*) and pitted cancellate (*Stanisicaropa* and *Biomphalopa*) patterns emerging in the protoconch architecture. This reinforces



FIG. 11. MEQ *charopid* habitats. **A**, Moist montane rainforest of Broken R., Eungella NP, MEQ. **B**, Drier araucarian rainforest of the Whitsunday Islands, MEQ. **C**, Semi-arid vine thicket of Hazelwood Gorge near Eungella Dam, MEQ.

Stanisic's view (2016) that all protoconch descriptions need to be completed by analysis of scanning electron micrographs.

Gyrocochlea-grade MEQ charopids are chiefly restricted to montane and surrounding moist rainforest habitats of the Clarke-Connors Ra. and the drier coastal araucarian forests of the Conway Ra., Mt Dryander and nearby Whitsunday islands (Fig. 11). A volcanic hotspot from 32 million years ago at Cape Hillsborough provides a similar forest ecosystem to that of the Whitsundays and is the exception to this as no *Gyrocochlea*-grade species have been found there to date. The semi-evergreen vine thickets of the Eungella Dam environs and notophyll vine forests in the Funnel Ck-Bell's Gap area also support *Gyrocochlea*-grade species. Land clearing and farming in the Proserpine-Sarina lowlands has restricted charopids to remnant patches of vine thicket but no *Gyrocochlea*grade species has hitherto been discovered in these habitats.

The importance of the Clarke-Connors Ra. and Whitsunday biogeographic provinces as hotspots of charopid endemism raises questions of their evolutionary relationships. Mid-eastern Queensland is separated from the humid, wet tropics and the dry to moist subtropical forests of SEQ by two dry corridors of open eucalypt forest: the Burdekin-Lynd Gap in the north and the St Lawrence Gap in the south. This has isolated the region into refugial pockets of rainforest (Webb & Tracey 1981; Bryant et al. 2016) and probably affected subsequent charopid distribution including that of the Gyrocochleagrade species. The nine species dealt with in this study represent one known genus and seven new genera including the re-assignment of the three previously known 'Gyrocochlea' species from this area. This indicates a level of charopid diversity previously unknown within the MEQ area. The extralimital relationships of these species have yet to be established but the examination of numerous protoconch micrographs undertaken by the author as part of a related study (Holcroft 2018) strongly suggests that these will chiefly be to species in adjacent bioregions to the south. Detailed investigation of Gyrocochlea-grade species, particularly in the Calliope-Rockhampton-Byfield area as well as the off-lying islands of the Cumberland, South Cumberland and Northumberland groups should be a priority for future research. However, relatives of at least one of the Gyrocochlea-grade species, Biomphalopa recava, do occur in adjacent bioregions but in northern Queensland. This MEQ-NEQ relationship also needs to be reexamined in the detail outlined herein and by Holcroft (2018).

While this study is focused on Gyrocochleagrade charopids, many non-Gyrocochleagrade MEQ charopids are also endemic to the region and similarly appear related to species in the SEQ and the Wet Tropics (Holcroft unpublished). The north-south geographical patterns of charopid lineages that have been identified in recent charopid research (Shea et al. 2012; Holcroft 2018) would suggest that continued research into the Charopidae could contribute significantly to an improved biogeographic understanding of eastern Australia.

Conservation

Snails including the Charopidae, are often overlooked in conservation assessments. With their ability to be responsive to environmental change, these tiny charopids make excellent indicators of terrestrial biodiversity and ecosystem health (Stanisic 1990; Stanisic & Ponder 2004; Shea et al. 2012). Their endemism in particular has significant impact for all the environments in which they are found. Concerns are being raised about clearing of rainforests (McAlpine et al. 2002) and the impact of controlled burn-offs particularly in the Eungella NP where at the point where this national park is no wider than one kilometre, the gradual encroaching of the land affected by these fires into the pristine rainforest could well have the potential to eradicate entire species of charopid.

While none of the MEQ charopids have received conservation protection under legislation, their preference for humid rainforests and vine thickets indicates that conservation of these areas is crucial for the snails' continued survival. Many of the mainland coastal areas have been cleared for farming and the high levels of endemicity this group display would suggest that some species may have already been lost. Much of the remaining rainforest is now situated in National Parks and State Forests which will protect the diversity of these charopids.

ACKNOWLEDGMENTS

First and foremost, the research presented in this paper could not have been achieved without the constant encouragement and constructive feedback of Dr John Stanisic, an expert in his own right on Charopidae and to whom I owe special thanks. Dr Stanisic also supervised and helped with the dissection of the two MEQ species. I am most grateful to my supervisors, Professor Jane Hughes and Dr Chris Burwell from Griffith University, for their ongoing feedback, support and encouragement. I wish to acknowledge Geoff Thompson of the Digital Imaging Unit, Queensland Museum for providing the high quality colour images of the species studied herein. The comprehensive feedback from the two reviewers made a significant difference and I thank them for their time and recommendations for improvement.

LITERATURE CITED

- Bishop, M.J. 1981. The biogeography and evolution of Australian land snails. In A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 924-954. (W. Junk Publishers: The Hague, Netherlands).
- Bonham, K.J. 2003. *Biogeography of Tasmanian native land snails*. PhD thesis, (University of Tasmania: Tasmania).
- Bryant, L.M. & Krosch, M.T. 2016. Lines in the land. a review of evidence for eastern Australia's major biogeographical barriers to closed forest taxa. *Biological Journal of the Linnean Society* 119: 238-264.
- Bureau of Meteorology. 2017. Climate statistics for Australian locations. Available online at http:// www.bom.gov.au [Accessed on 1 June 2017.]
- Forbes, E. 1851. On the Mollusca collected by Mr Macgillivray during the voyage of the Rattlesnake. Pp. 360-386 In, Macgillivray, J. (ed.) Narrative of the Voyage of the H.M.S. Rattlesnake commanded by the late Captain Owen Stanley, during the years 1846-1850., Volume 2. (T & W Boone: London).
- Hedley, C. 1912. On some land shells collected in Queensland by Mr. Sidney W. Jackson. *Proceedings of the Linnean Society of New South Wales* 37: 253-270.
- 1924. Some notes on Australian land shells. *Australian Zoologist* **3**: 215-222.
- Holcroft, L. 2017. Protoconchs and possibilities: elucidating the diversity of mid-eastern Queensland pinwheel snails (Eupulmonata:

Charopidae) using aspects of shell morphology. *The Malacological Society of Australasia Newsletter* **160**, 1-6.

- 2018. Protoconch sculpture as a taxonomic tool in Australian charopid systematics (Gastropoda: Eupulmonata: Charopidae), *Molluscan Research*, https://doi.org/10.1080/13235818.2 017.1409069.
- Hyman, I.T. & Stanisic, J. 2005. New charopid landsnails, chiefly from limestone outcrops in eastern New South Wales (Eupulmonata: Charopidae). *Memoirs of the Queensland Museum* 50: 219-302.
- Iredale, T. 1937a. A basic list of the land Mollusca of Australia. *Australian Zoologist* 8: 287-333.
- 1937b. An annotated checklist of the land shells of south and central Australia. *The South Australian Naturalist* **18**: 6-56.
- McAlpine, C.A., Fensham, R.J. & Temple-Smith, D.E., 2002, Biodiversity conservation and vegetation clearing in Queensland: principles and thresholds. *The Rangeland Journal* 24: 36-55 https://doi.org/10.1071/RJ02002.
- Shea, M., Colgan, D. & Stanisic, J. 2012. Systematics of the landsnail genus *Gyrocochlea* and relatives (Mollusca: Charopidae). *Zootaxa* 3585: 1-109.
- Smith, B.J. 1992. Non-marine Mollusca. In Houston, W.W.K. (ed.) Zoological Catalogue of Australia. (Australian Government Publishing Service: Canberra). Vol. 8 xii 408 pp.
- Smith, B.J. & Kershaw, R.C. 1979. Field guide to the non-marine molluscs of south eastern Australia. (Australian National University Press: Canberra) 285pp.
- Solem, A. 1983. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography. (Field Museum: Chicago).
- Stanisic, J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca:

Pulmonata) from sub-tropical rainforests. *Memoirs of the Queensland Museum* **30**: 1-241.

- 1998. Family Charopidae. Pp. 1097-1099 in Beesley, P. L., Ross, G. J. B. & Wells, A. (eds) Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5. Part B viii, 565-1234pp (CSIRO Publishing: Melbourne).
- 2016. Two new species of Pinwheel Snail from Queensland and a redescription and generic reassignment of *Gyrocochlea myora* Stanisic, 2010 (Gastropod: Eupulmonata: Charopidae), *Memoirs* of the Queensland Museum-Nature **60**: 1-12.
- Stanisic, J. & Ponder, W.F. 2004. Forest snails in eastern Australia: one aspect of the other 99%. Pp. 127-149 in D. Lunney (ed.) Conservation of Australia's Forest Fauna. (Royal Zoological Society of New South Wales: Mosman) https:// doi.org/10.7882/FS.2004.011.
- Stanisic, J., Shea, M., Potter, D. & Griffiths, O. 2010. Australian Land Snails Volume 1: A Field Guide to Eastern Australian Species. (Bioculture Press: Mauritius) 596pp.
- Stanisic, J., Shea, M., Potter, D. & Griffiths, O. 2017. Australian Land Snails Volume 2: A Field Guide to southern, central and western species. (Bioculture Press: Mauritius) 594pp.
- Van Bruggen, A.C. 1980. Gondwanaland connections in the terrestrial molluscs of Africa and Australia. *Journal of the Malacological Society of Australia* **4**: 215-222.
- Webb, L. J. & Tracy, J.G. 1981. Rainforests: patterns and change, *In*, A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 606-694. (W. Junk Publishers: The Hague, Netherlands) https:// doi.org/10.1007/978-94-009-8629-9_22.
- Willmott, W. F. 2006. Rocks and landscapes of the national parks of central Queensland, (Geological Society of Australia, Queensland Division: Brisbane).

Taxa	Registration number	SEM images taken	Anatomical dissection
Amfractaropa bretti	QMM011716	\checkmark	
Biomphalopa recava	QMMO39878	\checkmark	
	QMM085117	\checkmark	
Comularopa georginae	QMM059546	\checkmark	
Gyrocochlea paucilamellata	QMMO16546	\checkmark	
Gyrocochlea vinitincta	AMSC139752	\checkmark	
Radiolaropa eungella	QMMO36099	\checkmark	
	QMMO95343	\checkmark	
Nodularopa samanthae	QMMO13081	\checkmark	
,	QMM077397	\checkmark	
Radiolaropa danieli	QMM011745	\checkmark	
Stanisicaropa chambersae	QMM078961	\checkmark	\checkmark
	QMMO35619	\checkmark	
	QMMO85097	\checkmark	
	QMM085093	\checkmark	
Whitcochlea iuloidea	QMM085338	\checkmark	\checkmark
	QMM085334	\checkmark	
	QMMO85183	\checkmark	
	QMM074108	\checkmark	
	QMMO65943	\checkmark	
	QMMO65833	\checkmark	
	QMMO64807	\checkmark	
	QMMO59193	\checkmark	
	QMMO39879	\checkmark	
	QMMO6342	\checkmark	
	JW3444	\checkmark	
Xenoropa wigtonensis	QMM085180	\checkmark	
, 0	QMM070431	\checkmark	

APPENDIX 1. Specimens included in SEM analysis and anatomical dissection

Holcroft, L.

APPENDIX 2. Measurements of MEQ Gyrocochlea-grade species

Taxon	Reg #	D	н	U	AH	AW	PD	WWB	T 1	H/D	D/U	# Whorls
Stanisicaropa chambersae	QMMO13456	5.41	2.87	1.80	1.89	1.56	0.49	20.00	52.00	0.53	3.00	4.000
	QMMO11758	4.92	2.79	1.64	2.13	1.72	0.66	23.00	51.00	0.57	3.00	4.500
	QMMO85079	4.75	2.46	1.31	2.05	1.56	0.66	22.00	61.00	0.52	3.63	4.000
	QMMO35619	5.49	2.95	1.48	2.38	1.89	0.49	19.00	50.00	0.54	3.72	4.125
	QMMO13071	5.33	2.95	1.97	2.38	1.64	0.49	17.00	57.00	0.55	2.71	4.250
	QMM078961	4.92	2.62	1.56	2.05	1.72	0.49	17.00	51.00	0.53	3.16	4.125
	QMM078961	4.43	2.70	1.72	1.97	1.39	0.49	17.00	49.00	0.61	2.57	4.125
	QMM078961	5.57	2.87	1.80	2.05	1.80	0.41	21.00	57.00	0.51	3.09	4.125
	QMM078961	4.92	2.79	1.64	1.97	1.72	0.49	20.00	52.00	0.57	3.00	4.375
	QMM078961	5.49	3.03	1.80	2.05	1.56	0.66	21.00	55.00	0.55	3.05	4.500
	QMM078961	5.08	2.95	1.72	2.38	1.72	0.66	22.00	60.00	0.58	2.95	4.375
	QMMO11758	4.92	2.62	1.56	2.05	1.56	0.57	22.00	42.00	0.53	3.16	4.250
	QMMO11714	4.26	2.54	1.39	2.05	1.56	0.66	17.00	55.00	0.60	3.06	4.000
MEAN: Stanisicaropa chambersae	13 adult specimens	5.04	2.78	1.65	2.11	1.65	0.55	19.85	53.23	0.55	3.08	4.212
Radiolaropa danieli	QMMO35807	2.87	1.89	1.56	1.48	0.98	0.49	42.00	76.00	0.66	1.84	3.750
,	QMMO35807	2.87	1.80	1.15	1.56	1.31	0.49	42.00	85.00	0.63	2.50	4.000
	QMMO85340	3.69	2.05	1.07	1.64	1.31	0.49	46.00	67.00	0.56	3.46	4.125
MEAN: Radiolaropa danieli	3 adult specimens	3.14	1.91	1.26	1.56	1.20	0.49	43.33	76.00	0.61	2.60	3.96
Radiolaropa eungella	QMMO85343	3.11	1.64	1.07	1.48	1.07	0.49	38.00	86.00	0.53	2.92	3.875
	QMMO36099	2.95	1.56	1.23	1.23	0.98	0.49	39.00	95.00	0.53	2.40	4.125
MEAN: Radiolaropa eungella	2 adult specimens	3.03	1.60	1.15	1.35	1.02	0.49	38.50	90.50	0.53	2.66	4.00
Whitcochlea iuloidea	QMMO64807	5.57	2.54	2.05	2.21	1.80	0.57	24.00	54.00	0.46	2.72	4.750
(Long I)	QMMO64807	5.16	2.30	2.05	2.13	1.39	0.66	21.00	53.00	0.44	2.52	4.500
	QMMO64881	5.66	1.89	1.89	2.13	1.72	0.57	30.00	49.00	0.33	3.00	4.500
	QMMO74082	5.66	2.46	2.13	2.05	1.56	0.66	24.00	55.00	0.43	2.65	4.250
	QMMO74082	5.41	2.62	2.05	2.05	1.56	0.66	25.00	53.00	0.48	2.64	4.500
	QMMO74082	5.41	2.62	2.13	2.05	1.31	0.74	26.00	53.00	0.48	2.54	4.250
	QMMO85338	5.49	2.95	1.89	2.05	1.97	0.74	26.00	44.00	0.54	2.91	4.625
	QMMO85338	4.84	2.38	1.72	1.72	0.90	0.66	22.00	51.00	0.49	2.81	4.625
	QMMO85338	5.00	2.38	1.80	2.13	1.97	0.66	19.00	52.00	0.48	2.77	4.000
	QMMO85338	5.25	1.80	1.97	1.72	1.48	0.66	23.00	48.00	0.34	2.67	4.500
	QMMO85338	5.33	2.62	2.13	2.05	1.48	0.66	24.00	53.00	0.49	2.50	4.500
	QMM073834	5.57	3.11	2.05	2.21	1.64	0.57	26.00	51.00	0.56	2.72	4.750
	QMMO85338	4.92	2.79	1.80	1.97	1.48	0.57	24.00	48.00	0.53	2.73	4.250
Whitcochlea iuloidea												
	QMMO6342	4.84	2.70	1.72	2.05	1.64	0.57	25.00	51.00	0.56	2.81	4.250
(Conway Range)												
	QMMO6342	4.67	2.46	1.56	2.05	1.64	0.49	27.00	51.00	0.53	3.00	4.375
	QMMO6342	4.51	2.21	1.64	2.13	1.56	0.49	27.00	52.00	0.49	2.75	4.250
	QMMO6342	4.51	2.46	1.48	2.05	1.31	0.57	28.00	52.00	0.55	3.06	4.125
	QMMO6342	4.10	2.13	1.56	1.97	1.39	0.49	27.00	59.00	0.52	2.63	4.000
	QMMO6342	4.26	2.30	1.39	2.05	1.48	0.49	27.00	55.00	0.54	3.06	4.250
	QMMO6342	4.34	2.46	1.39	1.97	1.56	0.49	22.00	60.00	0.57	3.12	4.250

continued...

Taxon	Reg #	D	н	U	AH	AW	PD	WWB	T1	H/D	D/U	# Whorls
	OMMO6342	3.77	2.30	1.48	1.97	1.39	0.49	22.00	60.00	0.61	2.56	4.000
	OMM06342	3.85	2.13	1.48	1.89	1.31	0.49	22.00	46.00	0.55	2.61	4.000
	IW1449	3.85	2.54	1.64	1.97	1.56	0.41	32.00	66.00	0.66	2.35	4.125
	OMMO19928	3.77	2.70	1.56	1.97	1.72	0.57	30.00	57.00	0.72	2.42	4.375
	OMMO20143	3.61	2.13	1.64	1.72	1.23	0.57	30.00	62.00	0.59	2.20	4.250
	~ OMM06341	4.10	2.38	1.64	1.72	1.31	0.49	24.00	61.00	0.58	2.50	4.250
	QMM06341	4.51	2.46	1.64	1.97	1.64	0.57	29.00	54.00	0.55	2.75	4.375
	OMM085124	4 43	2.21	1.39	1.80	1.56	0.57	25.00	59.00	0.50	3.18	4.375
	OMM035357	4 92	2 79	1.64	1.72	1.39	0.57	33.00	59.00	0.57	3.00	4 375
	OMM035357	4 84	2.46	1.56	2.05	1.56	0.57	26.00	59.00	0.51	3 11	4 250
	IW1512	4.51	2.38	1.80	1.00	1.64	0.57	25.00	49.00	0.53	2.50	4.500
	IW1512	4 84	2.46	2.13	1.97	1.56	0.66	23.00	48.00	0.51	2.27	4 000
	IW1512	4 18	2.13	1.64	1.97	1.56	0.57	23.00	45.00	0.51	2.55	4 250
	IW1512	4.26	2.10	1.56	1.64	1.50	0.57	24.00	50.00	0.54	2.00	4 250
	OMM035357	4 18	2.20	1 39	1.01	1.15	0.57	21.00	59.00	0.53	3.00	4 250
Whitcochlea juloidea	QMMO85186	4.51	2.62	1.64	1.89	1.56	0.57	25.00	46.00	0.58	2.75	4.375
(Gloucester Island)	QMM074108	4.43	2.05	1.56	2.05	1.80	0.57	26.00	45.00	0.46	2.84	4.000
Whitcochlea	QMMO65833	3.93	2.46	1.56	1.97	1.23	0.66	33.00	51.00	0.63	2.53	4.125
(Hamilton Island)	QMMO85182	4.51	2.46	1.64	1.80	1.48	0.57	30.00	57.00	0.55	2.75	4.250
Whitcochlea iuloidea	QMMO85183	4.67	2.46	1.64	1.97	1.48	0.57	24.00	51.00	0.53	2.85	4.375
(Peter Faust Dam)	QMMO35569	5.00	2.87	1.64	1.89	1.23	0.82	22.00		0.57	3.05	4.125
	QMMO35569	4.84	2.70	1.64	1.80	1.48	0.66	23.00		0.56	2.95	4.250
Whitcochlea iuloidea	QMMO65943	5.00	2.62	1.64	2.05	1.64	0.66	37.00	53.00	0.52	3.05	4.250
(Whitsunday Is)	QMM085184	4.10	2.21	1.48	1.89	1.48	0.57	30.00	51.00	0.54	2.78	4.000
	QMMO65943	4.26	2.70	1.48	2.05	1.64	0.49	31.00	56.00	0.63	2.89	4.125
	QMMO65923	4.84	2.62	1.64	1.80	1.64	0.66	36.00	52.00	0.54	2.95	4.125
	QMMO65923	4.51	2.38	1.48	1.80	1.39	0.66	35.00	52.00	0.53	3.06	4.125
Whitcochlea iuloidea	JW3857	4.92	2.70	1.72	2.13	1.80	0.74	23.00	51.00	0.55	2.86	4.125
(Proserpine R)	JW3857	4.34	2.46	1.56	1.89	1.56	0.57	25.00	53.00	0.57	2.79	4.125
	QMM085185	4.75	2.46	1.56	1.64	1.31	0.57	21.00	52.00	0.52	3.05	4.250
Whitcochlea iuloidea	QMMO35560	5.41	3.03	1.80	2.21	2.05	0.57	27.00	45.00	0.56	3.00	4.500
(Mt Dryander)	QMMO35560	4.92	2.70	1.48	2.05	1.80	0.57	26.00	46.00	0.55	3.33	4.250
	AMSC140445	4.75	2.62	1.97	2.13	1.48	0.57	22.00	50.00	0.55	2.42	4.250
	AMSC140445	4.59	2.38	1.80	2.05	1.56	0.57	21.00	49.00	0.52	2.55	4.250
	AMSC140445	4.92	2.54	2.05	2.05	1.72	0.74	19.00	53.00	0.52	2.40	4.000
	AMSC140445	4.43	2.21	1.80	1.97	1.64	0.49	19.00	52.00	0.50	2.45	4.250
	JW3857	5.33	2.87	1.64	2.13	1.80	0.74	26.00	45.00	0.54	3.25	4.500
	JW3857	5.33	2.87	1.89	2.13	1.80	0.57	31.00	49.00	0.54	2.83	4.675
	JW3857	5.33	3.03	1.80	2.21	1.89	0.66	23.00	49.00	0.57	2.95	4.675
	JW3857	4.84	2.79	1.80	2.13	1.97	0.66	22.00	48.00	0.58	2.68	4.375
	JW3857	4.67	2.62	1.64	1.97	1.56	0.57	24.00	46.00	0.56	2.85	4.375
	JW3857	4.84	2.70	1.64	2.05	1.89	0.57	22.00	51.00	0.56	2.95	4.500
	JW3857	4.92	2.46	1.48	2.05	1.39	0.57	26.00	50.00	0.50	3.33	4.500
	JW3857	4.84	2.54	1.56	1.97	1.72	0.74	26.00	43.00	0.53	3.11	4.500
	JW3857	4.92	2.70	1.64	2.05	1.80	0.57	27.00	52.00	0.55	3.00	4.500
Whitcochlea iuloidea	JW3444	5.41	2.87	2.05	2.05	1.72	0.74	27.00	45.00	0.53	2.64	4.250

continued...

Holcroft, L.

Taxon	Reg #	D	н	U	AH	AW	PD	WWB	T 1	H/D	D/U	# Whorls
(Mt Jukes)	JW3444	5.00	2.79	1.64	2.30	1.39	0.57	26.00	51.00	0.56	3.05	4.500
	JW3444	4.92	2.62	1.80	2.30	1.72	0.66	0.00	0.00	0.53	2.73	4.375
MEAN: Whitcochlea iuloidea	68 adult specimens	4.71	2.54	1.64	1.97	1.55	0.61	25.57	44.63	0.55	2.83	4.24
Xenoropa wigtonensis	QMMO70431	5.90	2.79	2.05	1.80	2.30	0.82	49.00	68.00	0.47	2.88	4.375
	QMMO85180	6.15	2.95	1.97	2.38	1.72	0.74	54.00	67.00	0.48	3.13	4.375
MEAN: Xenoropa wigtonensis	2 adult specimens	6.02	2.87	2.01	2.09	2.01	0.78	51.50	67.50	0.48	3.00	4.375
Comularopa georginae	QMMO59546	2.30	1.31	0.66	0.90	0.66	0.41	66.00	132.00	0.57	3.50	3.875
MEAN: Comularopa georginae	1 adult specimen	2.30	1.31	0.66	0.90	0.66	0.41	66.00	132.00	0.57	3.50	3.875
Nodularopa samanthae	QMM077397	2.79	1.64	1.07	1.39	1.15	0.49	42.00	95.00	0.59	2.62	4.000
	QMMO11745 QMMO13081	3.61	2.05	1.31	2.05	1.64	0.49	44.00	60.00	0.57	2.75	4.240
MEAN: Nodularopa samanthae	3 adult specimens	3.20	1.84	1.19	1.72	1.39	0.49	43.00	77.50	0.58	2.68	4.12
Biomphalopa recava	QMMO11749	3.28	1.80	1.48	1.48	0.74	0.49	26.00	44.00	0.55	2.22	4.250
	QMMO39878	4.18	2.21	1.89	1.97	1.07	0.57	20.00	40.00	0.53	2.22	4.000
	QMMO36093	4.02	2.05	1.80	1.72	1.15	0.57	30.00	50.00	0.51	2.23	4.250
	QMMO13073	4.67	2.70	2.46	2.13	1.48	0.57	22.00	37.00	0.58	1.90	5.125
	QMMO85117	3.11	1.80	1.56	1.64	0.74	0.57	16.00	38.00	0.58	2.00	4.250
	AMSC140230	3.85	2.46	1.89	1.97	1.23	0.49	22.00	36.00	0.64	2.04	4.750
	AMSC140230	4.10	2.46	2.05	2.05	1.23	0.57	21.00	37.00	0.60	2.00	4.000
MEAN: Biomphalopa recava	7 adult specimens	3.89	2.21	1.87	1.85	1.09	0.55	22.43	40.29	0.57	2.09	4.375
Amfractaropa bretti	QMMO11716	3.52	1.80	1.07	1.15	1.23	0.49	44.00	121.00	0.51	3.31	4.125
	QMMO11716	2.87	1.48	0.57	1.39	1.15	0.49	37.00	111.00	0.51	5.00	4.000
	QMMO59545	3.28	1.72	1.07	1.48	1.15	0.49	39.00	105.00	0.53	3.08	4.125
	QMMO11716	2.95	1.39	0.98	1.15	1.07	0.49	43.00	100.00	0.47	3.00	3.375
	AMSC140230	3.03	1.64	0.82	1.23	0.90	0.49	41.00	83.00	0.54	3.70	4.000
MEAN: Amfractaropa bretti	5 adult specimens	3.13	1.61	0.90	1.28	1.10	0.49	40.80	104.00	0.51	3.62	3.93